

XXVIII.—*On the Significance of certain Characters in some Charadriine genera, with a provisional classification of the Order Charadriiformes.* By PERCY R. LOWE, M.B.O.U.

(Plate VI. & Text-figures 10–12.)

I PROPOSE to deal first with what might be called the “Golden-Plover Association,” an assemblage comprised of the following species and subspecies :—

- The Golden Plover, *Pluvialis apricarius apricarius* (L.).
- The British Golden Plover, *P. apricarius oreophilus* Meinertz.
- The American Golden Plover, *P. dominicus dominicus* (Müller).
- The Pacific Golden Plover, *P. dominicus fulvus* (Gmelin).
- The Grey Plover, *Squatarola squatarola squatarola* (Linn.).
- The American Grey Plover, *S. squatarola cynosuroides* Thayer & Bangs.

Considered as a single association, this Plover-group would appear to be admirably specialised, as far as colour-pattern is concerned, for the regions which may be said to be its typical home—viz., the Tundras of the Old World and the Barren-grounds of the New. In the Tundras one of the most characteristic features of the flora is the lichen known as Reindeer Moss (*Cladonia rangiferina*), while in the Barren-grounds true mosses are met with. On the face of it, nothing could seem to be more admirably adapted to such a floral background than the colour-pattern of the dorsal surface of the adult or nestling of any of the above-mentioned species or subspecies; indeed, some might be inclined to quote it as a wonderful illustration of the direct evolutionary influence of the immediate tundra environment aided by natural selection.

We may pause, however, to reflect that, firstly, this immediate environment on the nesting-grounds of these

arctic Tundras is not, as we have just noted, identical in the Old and New Worlds; secondly, quite a number of other Limicolæ, with very different colour-patterns, appear to get on just as well in the nesting-season in apparently identical environmental surroundings, differing species being even found in the closest juxtaposition; thirdly, Golden Plovers breed at the present time in areas (*e.g.* in the British Isles) which were once Tundras but are now, with the return of more genial conditions, grass- or heather-clad moorlands, an immediate environment which could not be said to bear a very close resemblance to that of the Tundras; and fourthly, both the Grey and the Golden Plovers are equally at home in the Old and New Worlds where, as we have seen, the floral picture presented by the nesting-areas is not identical.

In addition to these facts, we may point out that the colour-pattern in the downy nestling of the Grey differs from that of the Golden Plover; for, apart from details, the Grey Plover nestling is conspicuous for the white collar at the back of the neck, a feature entirely wanting in the Golden nestling; and it is interesting to note that this character is very typical of the nestlings of the Vanellinæ (*Vanellus* being a familiar instance) in whatever part of the world they are met with.

The same character is met with in the nestlings of the Ringed-Plover Association (*Charadrius = ~~Aegialitis~~, olim*); so that here we have a conspicuous colour-pattern character occurring in the nestlings of three distinct groups of Plovers; groups, moreover, which are world-wide in distribution and in which the character of the immediate nesting-ground is anything but similar; so that, if we are justified in drawing any conclusion at all, it is that this white neck-ring character in the nestlings of all the heterogeneous forms alluded to, is a factor which has been inherited from some common pluvialine ancestor, and has not arisen as the direct result of environment aided by natural selection.

Before passing on to our more particular object, there are other points worthy of a moment's consideration. The

Tundras are and were presumably always associated with glacial conditions, and the various glacial onsets coincided with the Pleistocene, as far, at any rate, as the Northern Hemisphere and our immediate thesis is concerned. If, therefore, it is held that the colour-pattern typical of the Golden-Plover Association was the direct outcome of a response to the tundra environment, it follows that this colour-pattern is no older than the Pleistocene. It is, of course, impossible to prove the contrary. Colour-pattern in any particular phylum or group may have been, in the past, changeable and evanescent; yet, from the evidence which I shall presently produce, and from evidence which I have already produced*, there seems every reason to suspect that it may be even more persistent than bony structural characters; while as to the persistence of these last in birds, one has only to examine the series of fossil *Limicolæ* in the British Museum Collection to be deeply impressed—characters, for instance, may still be reproduced in the head of a humerus of, let us say, an *Erolia* or *Tringa* form of the present day which are, in the most minute degree, comparable to those of a like form as far back as the Miocene (say three or four million years ago). The characters, for instance, which differentiate the humerus of a fossil Miocene Plover from a Miocene Gull are amazingly similar to those of present-day forms.

If, then, we may presume, as I think we are entitled, that the colour-pattern characteristic of the "Golden-Plover Association" is older than the Pleistocene, it might well be asked where were situated the Miocene or Pliocene Tundras to fix such a colour-pattern (by the usually accepted means of natural selection and the survival of the fittest): for a study of the fossil Tertiary flora in circum-polar and arctic regions does not suggest tundra conditions: and we know that all through the Tertiary, Europe, at any rate, enjoyed a mild and at first even a tropical or a sub-tropical climate.

* *Ibis*, 1914, pp. 399-403; 1915, pp. 320-346.

Such reflections give pause for thought, and we have to seriously ask ourselves if the origin of characters such as colour-pattern (or indeed any characters) can be explained by a blind appeal to the old formulæ.

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To turn, however, from speculation, we find that although a single and striking form of colour-pattern (too well known to require noting here) is characteristic of the "Golden Plover group" regarded as a whole, this group in reality consists of two subgroups which have been distinguished by generic rank; that is to say, the Grey Plover has been relegated to the genus *Squatarola* and the Golden Plover to the genus *Pluvialis*.

The only reason which has been advanced by systematists for the recognition of the genus *Squatarola* is, so far as I am aware, the presence of a rudimentary hind-toe; while the author of the anatomical notes in 'The British Bird Book' has definitely stated in a footnote on page 573 that it is impossible to recognise such a genus at all. In reality, some rather remarkable anatomical characters, apparently hitherto overlooked, seem to fully justify the generic separation of the Grey from the Golden Plover. I am not immediately concerned, however, with the justification of either one or the other genus, but rather with the problem of the significance of the somewhat remarkable deep-seated differences which characterise the two groups.

These differences may be described as follows:—

In the first place, only two cervico-dorsal vertebræ with two free ribs are present in *Squatarola*, while in *Pluvialis* there are three. Here, at once, we find a meristic phenomenon which is difficult to explain by any appeal to the influence of either function or environment.

Turning to the skull we find:—

(a) That the lacrymals in *Squatarola* are strikingly different, being prominent out-jutting processes, almost Larine or Tringine in appearance; while in *Pluvialis* their outer margin is rounded and merged into the line of the orbital

rim, being continued forwards and inwards in a smooth and somewhat noticeable convexity in a manner somewhat reminiscent of *Vanellus* (text-figs. 10 *b* & 11 *b*).

(*b*) The interorbital space presents very distinct differences in the two forms. In *Squatarola* it is narrower both actually and relatively, while the raised corniced and everted orbital rim so characteristic of *Pluvialis* is not present; moreover, the grooves for the supra-orbital glands are not nearly so deep or defined as in *Pluvialis*, and the general arrangement here is Larine or Tringine (text-figs. 10 *b* & 11 *b*). In *Squatarola* there are no anterior foramina caudad of the lacrymals. They are well marked in *Pluvialis*, and this seems to be a Charadriine character. In *Squatarola* the inner margins of the grooves for the supra-orbital glands meet in the middle line of the vertex, forming a prominent sagittal ridge down the centre. In *Pluvialis* there is a fairly broad and clearly-marked smooth median depression down the centre of the interorbital space, which is not encroached upon by the supra-orbital grooves.

(*c*) Turning to the palatal plates, we find in *Squatarola* that the postero-external angle is rounded off (in some specimens much cut away). In *Pluvialis* the angle is squarer.

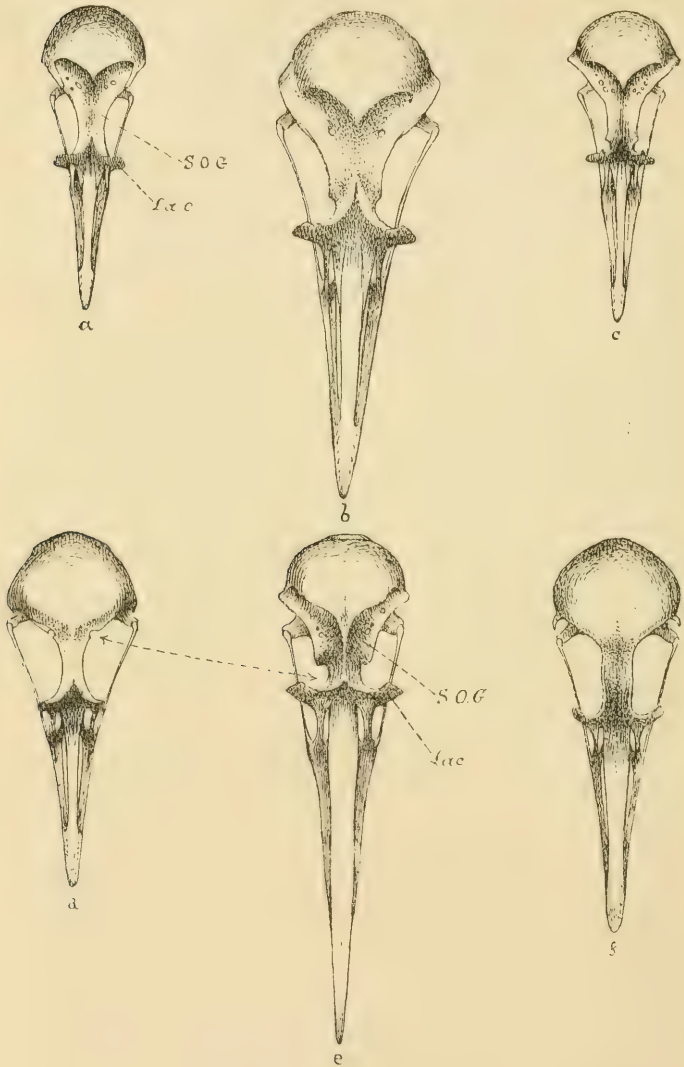
(*d*) In *Squatarola* the ectethmoid or antorbital plate is somewhat triangular in form, the extero-inferior angle representing the apex. In *Pluvialis* the antorbital plate has a quadrilateral form*.

(*e*) In *Squatarola* the descending process of the lacrymal falls perpendicularly to just touch the apex of the antorbital plate. In *Pluvialis* it runs along the outer margin but does not fuse with it.

(*f*) Turning to a comparison of the maxillo-palatines, we find that in the two forms under discussion these are not identical. In *Squatarola* they appear to be more closely applied to the pre-palatals, their posterior or free points being little separated from the palatal plate. In *Pluvialis*

* This, at any rate, is evident in perfectly ossified examples.

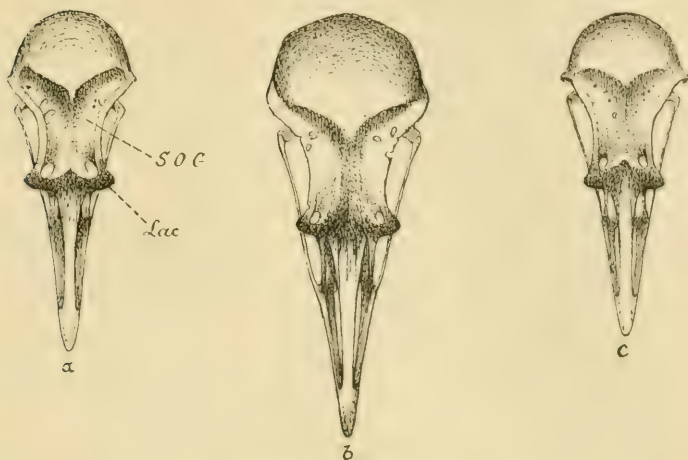
Text-figure 10.



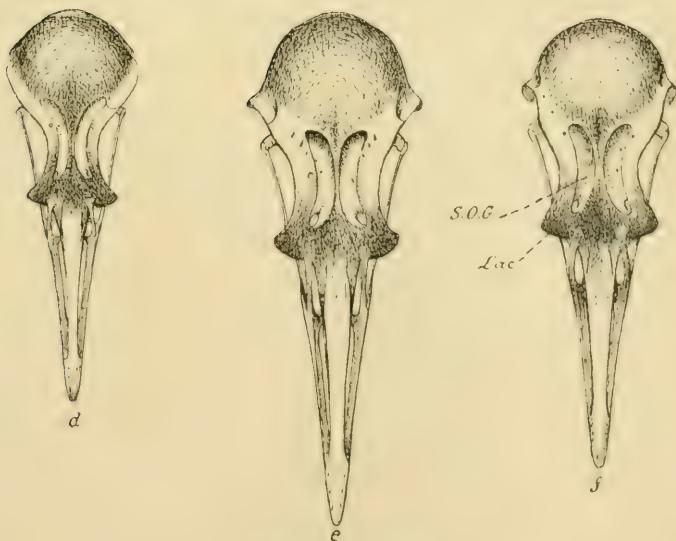
PRE-CHARADRIINÆ

Skulls of Pre-Charadriinæ.—*a.* *Leucopoli* *ruficapillus*; *b.* *Squatarola squatarola*; *c.* *Leucopoli* *alexandrinus*; *d.* *Arenaria interpres*; *e.* *Hæmatopus ostralegus*; *f.* *Aphriza virgata*. *S.O.G.* = Supra-orbital groove. *Lac.* = Lacrymal bone. All figures nat. size, except *e* which is two-thirds nat. size.

Text-figure 11.



CHARADRIINÆ



VANELLINÆ

Skulls of Charadriine and Vanelline.—*a.* *Charadrius cucullatus*; *b.* *Pluvialis pluvialis*; *c.* *Charadrius hiaticula*; *d.* *Eudromias morinellus*; *e.* *Chettusia leucura*; *f.* *Vanellus vanellus*. *S.O.G.* = Supra-orbital groove. *Lac.* = Lacrymal bone. All figures nat. size.

the free ends converge towards the middle line and underlie the vomer, so that that part of the vomerine process is hidden when these structures are viewed from the palatal aspect. The maxillo-palatines in *Pluvialis* are also more shell-like concavo-convex structures (or more scroll-like). The attachment to the palatal process of the premaxilla is less extensive than in *Squatarola*.

(g) In *Squatarola* I have noticed that the dentary margin of the premaxilla is not completely fused with the corresponding portion of the maxillo-palatine as it is in *Pluvialis*. This is a Larine as opposed to Pluvialine character.

(h) In *Squatarola* the postero-external angles of the basi-temporal plate end in two fairly conspicuous downwardly projecting processes of bone. These processes are but little evident in *Pluvialis*, but are quite characteristic of the Laridæ and Sternidæ. If well-prepared skeletons of the skulls of the two genera under discussion are compared, these differences are generally apparent. A similar distinction is noted between *Larus* and *Stercorarius*.

It is obvious, then, that even if we confine ourselves to characters noted in the skull, there are somewhat surprising anatomical differences in the two forms under discussion, especially if those differences are regarded from a generic point of view, and it is remembered that the leading or outstanding generic character which has been hitherto held to distinguish *Squatarola* from *Pluvialis* is the abortive hind-toe. It may well be that a good many of the characters referred to above are proportional characters, but it will be noted that they are proportional characters characteristic of various Limicoline groups, and in this respect *Squatarola* seems to present a complex of unit characters of a more mixed nature than *Pluvialis*, a complex now reminiscent of a purely Vaneline type, now Larine or Tringine or now Charadriine; so that we might apparently be justified in hazarding the opinion that *Squatarola* was an older or more generalised type which we might call Pluvialine or Pre-Charadriine; but to this point I shall return.

In the meanwhile it is a very noteworthy and I think highly interesting fact, that we apparently find an almost precisely similar condition of things in another adjacent group of Plovers. I refer to the "Ringed-Plover Association." By this association I mean a certain restricted group of the old heterogeneous collection comprised under the genus *Agialitis* (olim). This restricted group of Ringed Plovers may be divided into two subgroups to which the generic names *Charadrius* and *Leucopolius* have been applied. While by no means generally recognized, each of these genera has been characterised by well-marked superficial characters connected with the form of the bill, legs, and feet*.

In the genus *Charadrius* may be included such forms as :

- Charadrius hiaticula,*
- „ *dubius,*
- „ *placidus,*
- „ *melodus,*
- „ *semipalmatus,*

with two rather aberrant or specialised forms, *C. cucullatus* and *C. bicinctus*.

In the genus *Leucopolius* we may include :

- Leucopolius alexandrinus,*
- „ *nivosus,*
- „ *peroni,*
- „ *rujicapillus,*
- „ *marginatus,*
- „ *collaris,*
- „ *venustus.*

Now, just as in the case of *Squatarola* and *Pluvialis*, both the two genera, *Charadrius* and *Leucopolius*, are, as regards adult examples of the various species, linked together by possessing a similar well-marked colour-pattern, too well

* From an examination of skins, Messrs. Mathews and Iredale have insisted on these generic differences, and osteological characters prove them to have been thoroughly justified.

known to need description here but thoroughly characteristic of the "Ringed Plovers," although in *Leucopoliis* the colour-pattern is, so to speak, adumbrated—a point to be further noted (*cf.* Plate VI.)

As regards osteological features, we find a similar state of affairs as we did in the "Golden-Plover Association"; that is to say, the skulls of all the species of *Leucopoliis* examined* present features exactly reminiscent, if not identical, with *Squatarola*, while those of *Charadrius* resemble *Pluvialis* (*cf.* figures).

This is all the more remarkable when we consider the very great distances which separate the various species in either group. Thus in *Leucopoliis* we find *L. alexandrinus* breeding in Europe and Asia, *L. nivosus* in America, and *L. ruficapillus* in Australia; while as regards *Charadrius* we find in the case of *C. hiaticula* (Europe and America), *C. placidus* (China and Japan), *C. semipalmatus* (America), and *C. monachus* (Australia) equally astonishing distances separating the various forms.

In the case of the colour-pattern characteristic of the downy nestlings of the two groups, there is not only a quite obvious generic difference, but in each of the two genera there is an equally striking similarity between individual species no matter what the distance may be separating them; for instance, the coloration and the colour-pattern of the downy nestlings of *L. alexandrinus* (Europe), *L. nivosus* (America), and *L. ruficapillus* (Australia) are so precisely identical that, if the nestlings were inadvertently mixed, it would be all but, if not actually, impossible to separate them, and the same applies to the genus *Charadrius* (*cf.* Pl. VI.)

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Such, then, are the series of characters which we may observe to differentiate either of the two subgroups or genera into which the "Golden-Plover" and the "Ringed-Plover" associations may be divided—subgroups, it may again be noted, which in each case are obviously linked by phylogenetic characters, such as colour-pattern and anatomical

* See further on, p. 489.

similarities, into a larger whole, and as obviously differentiated into their respective genera.

It has been suggested that the anatomical differences which I have observed between the genera *Squatarola* and *Pluvialis*, as also between *Leucopoliis* and *Charadrius*, are merely the result of differences of function and habits; in reply to which we can only put the question—Are the habits and functions of the Grey and Golden Plovers or of the Kentish and Common Ringed Plovers so different that such striking cranial differences as we have depicted could conceivably have been produced, or was the environment of the Grey and Golden Plovers or of the Kentish and Common Ringed Plovers so different that it could possibly have called forth such anatomical differences in response to it?

If the suggestion is correct*, it is a very remarkable and astonishing fact that the habits and functions of the Grey Plover of the Tundras, the Kentish Plover of Europe, and the Red-necked Plover of Australia are so precisely alike that exactly similar cranial characters have in each case been separately evolved in response to them in the three forms, to say nothing about environment which presumably ought to be similar too, in order to support the argument.

The fact, too, that on the one hand the nestling Kentish Plover (*L. alexandrinus*) of Europe, the Snowy Plover (*L. nivosus*) of America, and the Red-necked Plover (*L. ruficapillus*) of Australia are so precisely alike, *inter se*, that one can only with difficulty be differentiated from the other, while on the other hand they are obviously differentiated from the nestlings of the Common Ringed Plover group (*C. hiaticula*, *dubius*, *semipalmatus*, *placidus*, &c.), which in turn are as like to one another as two rows of peas, seems to me to suggest phyletic rather than environmental influences (*cf.* Pl. VI.).

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What, then, is the explanation of these facts?

Any attempt at an answer must necessarily be speculative and suggestive; and my suggestion is that in either of the

* But see further on, pp. 488, 489.

two pairs of groups or genera whose differences *inter se* I have attempted to sketch we have depicted the early and late phases of a species, or a group of species, as evolved in TIME as opposed to SPACE. In other words, the Grey Plover group and the Kentish Plover group respectively belong to an earlier geologic horizon than the Golden Plover or the Common Ringed Plover group. In each of the four groups we have "varieties," subspecies, or species which may be regarded as more superficial present-day variations in relation to space; while on the other hand in each of the four groups we may observe deeper-seated structural characters which represent variations or mutations in relation to time.

Without, I venture to think, too great a strain on the imagination, these mutations in time, although not exactly comparable to the mutation of Waagen*, are suggestively similar; while the Grey and Golden Plover groups taken as a whole, or the Kentish Plover and Ringed Plover groups similarly regarded, may be compared in some sort to the phylum of modern Palæontology.

It is at least suggestive that in what I have termed in the case of either group "the early phase" we find osteological characters which are more generalised, or at any rate less specialised, than is the case in the later phase. It is obvious, for instance, that the six generalised Pluvialine forms figured under the title of Pre-Charadriine (p. 480) have a remarkable morphological likeness to Tringine or Larine† forms; while those figured as examples of the Charadriine would appear to be more specialised and more recent Pluvialine forms. Moreover, as I have previously noted above, in the colour-pattern characteristic of the species of all the Kentish Plover group (Plate VI. figs. 1-3) we seem to have an adumbration, or what may be (possibly somewhat

* Waagen, W. "Die Formenreihe des *Ammonites subradiatus*." Geognostisch-Palæontologisch Beiträge, Band ii. Heft ii. Nov. 1869, pp. 179-256. For a translation of his principles, cf. H. F. Osborn, "Origin of Single Characters as observed in Fossil and Living Animals and Plants," Amer. Nat. vol. xlix. No. 580, April 1915, p. 223.

† For a figure of the skull of *Larus canus* see Ibis, 1916, p. 326.

fancifully) compared to an artist's rough study or preliminary sketch, of the more firmly painted-in colour-pattern characteristic of the Common Ringed Plover group (*cf.* Plate VI. figs. 4-6).

These adumbrations or "studies" of colour-pattern I have often observed in other groups or phyla throughout the whole class of birds. To my fancy they have appeared to be "first attempts" on the part of Nature to produce the more completed sketch; and I think that there is ground for regarding the species of any group with these "adumbrated studies" of colour-pattern as being earlier in point of time of origin than those with more definitely completed colour-patterns. Moreover, such adumbrations of colour-pattern may be found in one part of the area of distribution of a group of species, while the more complete sketch may be found in another.

It will doubtless be answered that these faintly outlined "studies" are merely the result of environment caused, for example, by excess of light and aridity, or what not, in more barren or desert surroundings; but it might, I think, be just as reasonably argued that if a group or phylum of species belonging to an earlier geologic horizon and characterised by such a faintly marked colour-pattern sketch did not unconsciously seek an environment adapted to suit its case, it would be less likely to survive. In the case of the Kentish Plover group this presumably has been done in Europe, America, and Australia, and as a consequence they have survived.

But, it may be said, if we have a *Squatarola-Pluvialis* and a *Leucopoliis-Charadrius* group, each composed of sub-groups representative on the one hand of a more recent and on the other of an earlier geological horizon, the earlier forms (*Squatarola* and *Leucopoliis*) must be regarded as virtual "living fossils," and this, I think, we may take for granted; for of all classes Birds are the most amazingly persistent. In the case of Mammals, forms characteristic of past geologic horizons are for the most part extinct and fossilized. In the case of Birds it is open to doubt if we ornithologists sufficiently reflect what a number of living

forms still exist which are to all intents and purposes "living fossils" and belong to much earlier horizons than the present or indeed the Pleistocene or even much earlier periods.

As to the astonishing and remarkable persistence of birds, it may be worth while to record some remarks made by Shufeldt* upon the fossil *Palaeotringa littoralis* of Marsh, a Charadriiform type found as far back as the Cretaceous (Hornerstown, New Jersey). "In my opinion, this tibio-tarsus belonged to the skeleton of a medium-sized Gull and not to any Wader. Such characters as it presents in its imperfect condition are distinctly larine, and typically larine at that." Granting that this is correct, and allowing that Gulls are specialised offshoots of the Limicolæ, we can justly infer that Waders as Waders existed at least as far back as the Cretaceous.

I have myself examined examples of Tringine forms from the Middle Miocene which cannot be distinguished from the present-day Wood-Sandpiper; while fossil "Gulls" in the Lower Miocene from Allier in France in the British Museum collection present characters diagnostic of Terns and Limicolæ of the present day in the most minute and faithful degree. We need not be surprised, therefore, that while the mammalian Palæontologist has to look for his facts as regards mammalian history of the past in the fossils of various geologic horizons, the Ornithologist may by taking thought find the past history of Birds written to a great extent in the surviving forms of the present—indeed, since avian fossils are such a comparative rarity, it is self-evident that this is the only course open to him.

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In connection with the remarks on page 485 on the subject of morphology and function or habit, it is doubtless true that such anatomical features as the morphology of the supra-orbital grooves for the nasal glands, and the presence or

* "Fossil Birds in the Marsh Collection of Yale University." Trans. Connecticut Acad. Arts and Sci. vol. xix. Feb. 1915, p. 23.

absence of an anterior foramen leading to the nasal region had their primal origin in function or habit. Is there a single known morphological structure which has not the same origin, even such deep-lying ones as the vomer, palate, maxillo-palatine, or pterygoids, selected by Huxley for his system of avian classification? But when (to take one of the characters already noticed in the text) we find a certain type of nasal gland and a certain method of lubricating the Schneiderian membrane characteristic of a Wader-form like *Pluvialis apricarius* and an exactly similar arrangement in another form like *Charadrius hiaticula* or in forms like *Pluriorhynchus obscurus*, *Nesoceryx bicinctus* or *Charadrius cucullatus* (see text-figs. 10 & 11), it seems more reasonable to suppose that such precisely similar structures and physiological adaptations were inherited from some common ancestor rather than that they were separately acquired, in each case, as the result of exactly similar functional strains or habits acting independently. If this is so, such characters can, if selected with judgment, surely be regarded as evidence of affinity and utilized for the purpose of classification?

PROVISIONAL CLASSIFICATION OF THE CHARADRIIDÆ.

I am inclined, at any rate, to use these characters provisionally, along with others, in an attempt to classify the Charadriidæ. Working with the somewhat meagre material at present available, there are good reasons which lead one to think that the following genera might be grouped under a heading which I propose to term the PRE-CHARADRIINÆ, that is Pluvialine forms in which the lacrymals are free, and present conspicuous outwardly projecting processes very similar to what is seen in the Laridæ, and in which the foramen for the passage of the nasal duct is absent, its place being taken by a groove situated laterad of the anterior extremity of the frontals, an arrangement also characteristic of the Laridæ. To this group belong the following:—*Leucopolius (alexandrinus; occidentalis; ruficapillus; marginatus; peculiaris; sancte-helene; collaris; falklandicus)*: *Squatarola*:

Aphriza: *Hematopus*: *Pagolla (wilsonius)*: *Zonibyx (modestus)*: *Eupoda (asiatica)*: *Arenaria*.

Following the Pre-Charadriinæ would come the CHARADRIINÆ, that is, Pluvialine forms in which the lacrymals are not free but are merged in the supra-orbital rim, in which there is a conspicuous foramen for the nasal duct immediately caudad of the nasals, in which the supra-orbital grooves are deeply sculptured, often perforated with foramina, and extend well back to the anterior margin of the parietals, and in which the supra-orbital rim is conspicuously raised, everted, or corniced. In this group are included:—*Charadrius (hiaticula; dubius; semipalmatus; placidus; melodus; cucullatus)*: *Pluvialis*: *Cirripidesmus (mongolus)*: *Nesoceryx (bicinctus)*: *Pagoa (leschenaulti)*: *Afroxyechus (tricollaris)*.

Under another subfamily, for which I propose the name VANELLINÆ, we find the subjoined genera. The Vanellinæ may be defined as follows:—Pluvialine forms in which the lacrymals are not free but are merged in the even and rounded contours of the supra-orbital rim, which is not conspicuously raised, everted, or corniced (sometimes somewhat deepened), and in which the depressions for the nasal glands form two more or less short, simple (not sculptured or perforated), shallow, and more or less parallel grooves, with a single foramen at the anterior extremity. This group includes:—*Vanellus*: *Chactusia (gregaria)*: *Euhyas (leucura)*: *Eudromias (morinellus)*: *Podasocys (montanus)*: *Oxyechus (vociferus)*: *Eupoda (vereda)*: *Himantopus* (3 species): *Stephanibyx (inornatus)*: *Ptiloscelis (resplendens)*: *Hoploxypterus (cayanus)*: *Belonopterus (cayennensis)*: *Defilippia (crassirostris)*: *Xiphidiopterus (albiceps)*: *Tylibyx (melanocephalus)*: *Microsarcops (cinereus)*: *Lobivanellus (indicus)*: *Lobipluvia (malabarica)*: *Oreophilus (ruficollis)*.

So far as can be gathered from a study of the skulls of the Vanelline genera, all are so remarkably alike that it would even seem impossible to find characters with which to extricate a Dotterel group.

The three Vanelline forms figured on page 481 represent a very accurate sample of this similarity throughout the subfamily. I might also state here that no genus is mentioned throughout this paper, an example of which has not been studied osteologically.

Finally, we have the LOBIVANELLINÆ, which I define as Pluvialine forms similar to the Vanellinæ but with occipital fontanelles absent. In this subfamily would be included:—*Hoplopterus (spinosus)*: *Lobibyx (lobatus)*: *Zonijer (tricolor)*: and *Afribyx (senegallus)*.

It may eventually be found that several of the forms towards the latter end of the Vanelline list will have to be transferred to the Lobivanelline, as their skulls were incomplete in the occipital region, rendering it impossible to be certain if the occipital fontanelles were absent or present. My impression is that the Lobivanellinæ, as above defined, will be found to be confined to the Old World. At any rate, *Hoploxypterus cayanus*, *Oreophilus ruficollis*, and *Ptiloscelis resplendens* (New World forms) are definitely *not* Lobivanelline (*cf.* Sharpe, *Cat. Birds Brit. Mus.* vol. xxiv.). In any case I do not attach very much importance to this subfamily, and since this paper has been passing through the press I am inclined to regard it as a specialised offshoot from the Vanellinæ rather than an older branch as originally indicated in the phylogenetic tree (p. 493).

The Jacaninæ and Rynchæinæ would also be naturally included in the Charadriidæ. They are probably very ancient forms on the Vanelline side of the family (see text-fig. 12). In connection with the remarks already made on morphology and habit, it may be noted that in the Jacaninæ (one of the most aquatic of the Wader groups) the supra-orbital glands are absent.

The characteristic form and arrangement taken by the supra-orbital grooves (depressions for the nasal glands) and foramina (present or absent) for the conduction of the nasal duct leading to the nasal region, as well as of the form of the lacrymals and the general morphology of the inter-orbital region, is well seen in the text-figures on pp. 480, 481,

in which are depicted species, typical in each case of the Pre-Charadriinæ, Charadriinæ, and Vanellinæ.

The relative position and rank of the genera *Aphriza*, *Arenaria*, and *Hematopus* have always been a source of difficulty and a stumbling block in attempting a classification of the Charadriidæ. Their inclusion, along with *Leucopolius* and *Squatarola*, in my Pre-Charadriinæ seems not only to be indicated on the score of their general morphological similarity, but their generalised characters would appear to fit in with a Pre-Charadriine picture. There can be no doubt that they are not Scolopacine. On the other hand they are certainly not typical Plovers of the Charadriine or Vanelline group.

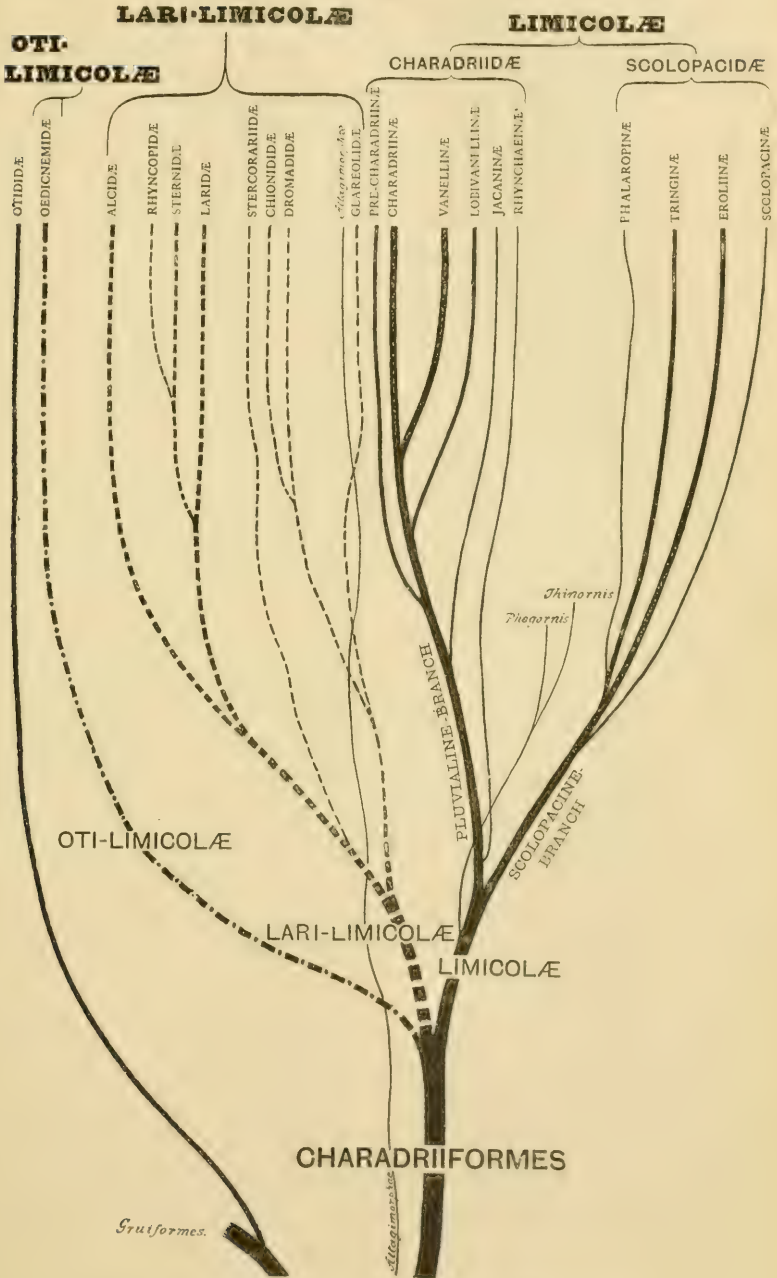
In order to more clearly indicate the relative position, constitution, and restrictions of my family Charadriidæ, it may perhaps be advisable to state that, so far as investigations have carried me at present, I regard the order Charadriiformes as dividing into three main branches (see text-fig. 12) or suborders, viz. :—

- (1) The Limicolæ = Charadriiformes in which the basipterygoid processes persist in the adult.
- (2) The Laro-Limicolæ = Charadriiformes in which the basipterygoid processes are lost in the adult.
- (3) The Oti-Limicolæ (Œdicnemidæ).

(1) LIMICOLÆ.—In the construction of the accompanying genealogical tree (page 493) my Limicoline main branch is represented as dividing into a Pluvialine and a Scolopacine secondary branch.

A. The Pluvialine division again divides into the Charadriinæ and Vanellinæ, while the subfamilies Pre-Charadriinæ, Lobivanellinæ, Jacaninæ, and Rhynchæinæ spring directly from the Pluvialine branch (the Pre-Charadriinæ ranging themselves alongside the Charadriinæ, and the Lobivanellinæ, Jacaninæ, and Rhynchæinæ on the side of the Vanellinæ). All six subfamilies are embraced under the family Charadriidæ.

Text-figure 12.



Hypothetical phylogenetic tree of the Charadriiformes.

- B. In like manner the Scolopacine branch divides into four secondary branches—the Phalaropinæ, Tringinæ, Erolinæ, and Scolopacinae, the last being represented as springing from the Erolinæ and the first from near the commencement of the Scolopacinae, the whole being embraced under the family Scolopacidae.
- (2) The LARO-LIMICOLÆ, the second of my three suborders into which the order Charadriiformes divides, consists of the following families:—Glareolidæ, Chionidæ, and Dromadidæ; the Stercorariidæ, Sternidæ, Rhyncopidæ, and Laridæ; and finally, the Alcidae. The various branches are depicted in the genealogical tree as being arranged in their probable closeness of affinity to the Charadriidæ or probably, to be more correct, in an ascending order of specialisation away from the Limicolæ, the less specialised modern representatives of the old Charadriiform types being here regarded as represented by the Erolinæ and Tringinæ.
- (3) The OTI-LIMICOLÆ.—As I am awaiting embryological and other material, I have no remarks to offer as yet upon this most difficult group. I have provisionally placed the *Ædienemidæ* alongside the *Otididæ* in such a way as to suggest convergent evolution, but the colour-pattern in the nestling suggests affinity with *Hematopus* or a derivation from a common ancestor. Moreover, I am not yet convinced that the *Otididæ* are gruiform birds, so that it is possible that they may eventually find a permanent resting place in my Oti-Limicolæ.

As regards *Thinornis* and *Phegornis*, I am, while awaiting further material, reluctant to commit myself, but I lean strongly to the opinion that they sprang from the Limicoline stem before that stem had divided into its Pluvialine and Scolopacine branches, and that it may therefore be eventually found impossible to include them in either the Charadriidæ

or Scolopacidae. It is conceivable that the primitive Charadriiform types exhibited very similar characters to those of *Thinornis*, *Phegornis*, and certain extinct Pacific forms. It is also very possible that *Rhyuchwa* should occupy a similar position in regard to springing from the main Limicoline stem (see alternative position).

As regards the Attagidae, the ægithognathous type of palate and other very interesting features would seem to warrant the view that they occupy a somewhat similar position in relation to the Charadriiformes that the Hemipodes do to the Galliformes and other groups. If this view is correct, they cannot be included in the Charadriiformes, but would form an annectant group—the Attagi-morphs, equivalent to the Turnico-morphs.

I have been moved to give this provisional and preliminary survey of my present conception of the relations of the Charadriiformes in the hope that by so doing I might possibly interest ornithologists in the collection of material necessary to complete a satisfactory review and classification.

XXIX.—*On the Birds collected by Mr. A. F. R. Wollaston during the First Mt. Everest Expedition.* By N. B. KINNEAR, M.B.O.U. With Notes by Mr. A. F. R. WOLLASTON.

(Plate VII.)

INTRODUCTION.

THE collection of bird-skins brought back by Mr. Wollaston from the Everest Expedition consists of 258 specimens referable to 59 species*.

As pointed out by Mr. Wollaston in his introductory remarks, birds could not be collected everywhere on account of the religious susceptibilities of the Tibetans. In addition

* For a map of the route and localities visited see 'Geographical Journal,' lix. no. 2, Febr. 1922.



TYPES OF CHARADIINÆ.

- | | | | | | |
|------------|-------------|---------------|------------|------------|--------------|
| 1, 1a, 1b. | LEUCOPOLIUS | RUFICAPILLUS. | 4, 4a, 4b. | CHARADRIUS | SEMPALMATUS. |
| 2. | " | NIVOSUS. | 5. | " | DUBIUS. |
| 3, 3a, 3b. | " | ALEXANDRINUS. | 6, 6a, 6b. | " | HIATICULA. |